Effects of density on the reproductive output of *Protea lepidocarpodendron*

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This paper explores the effects of density on the fecundity of *Protea lepidocarpodendron* (L.) L. This species is a non-sprouting, serotinous (canopy-stored seed) proteoid, endemic to the fynbos of the south-western Cape. It occurs naturally as the dominant overstorey species in populations encompassing a wide range of densities: it is therefore suitable for investigating current ideas which suggest that pre-fire population density is a major determinant of post-fire population size. Density-dependent effects on reproductive output and pre-dispersal seed predation were determined for *P. lepidocarpodendron* by recording annual cone and seed production, seed size, viability and pre-dispersal seed predation in 16-year-old dense (22 480 plants ha^{-1}), moderately dense (2 080 plants ha^{-1}) and sparse (160 plants ha^{-1}) stands. At the level of the individual plant, reproductive output showed considerable density-dependent decline, associated with smaller canopy volumes in the denser sites. Incidence of pre-dispersal seed predation showed a density-dependent increase probably due to shorter predator search times. However, our data indicated that density under-compensation was effective at the population level, resulting in greater viable seed production per hectare, and therefore potentially higher post-fire seedling numbers in the dense than in the sparse stands. This is contrary to recent research on proteoid communities burnt in autumn which showed lower seedling numbers in dense than in sparse stands. It was concluded that season of burn would be the overriding determinant of post-fire recruitment in the stands of *P. lepidocarpodendron* which we studied. Point diversity (number of understorey species m^{-2}) declined markedly with increasing proteoid overstorey density. This interaction could cause the local extinction of understorey species as a result of a fire regime which favours recruitment, and therefore thicket formation, of overstorey proteoids.

Hierdie artikel verduidelik die effek van digtheid op die vrugbaarheid van *Protea lepidocarpodendron* (L) L. Plante behorende tot hierdie spesie besit onvertakte stamme en is serotinies. Dit is endemies tot die fynbos van die Suidwestelike Kaap. Dit kom natuurlik as die dominante kruinstratumspesie voor in populasies waarvan digthede baie kan verskil: dit is derhalwe geskik om huidige opvattings te toets wat van die veronderstelling uitgaan dat die 'voorbrand'-populasiedigtheid 'n belangrike bepaler is van die 'nabrand'-populasiegrootte. Die invloed van digtheidafhanklikheid op reproduksie-uitset en saadparasitering voor saadvrystelling is vir *P. lepidocarpodendron* bepaal deur die jaarlikse blomkop en saadproduksie, saadgrootte, kiemkragtigheid en saadparasitering voor saadvrystelling aan te teken in digte stande (22 480 plante ha^{-1}), matig digte stande (2 080 plante ha^{-1}) en yl stande (160 plante ha^{-1}) wat 16 jaar oud is. Op die vlak van individuele plant, het reproduktiewe uitset 'n aansienlike digtheidafhanklikheidsafname getoon wat geassosieer word met kleiner kruinvolumes in digter areas. Die voorkoms van saadparasitering voor saadvrystelling het 'n digtheidafhanklikheidstoename getoon, waarskynlik vanweë 'n korter 'soektyd' van die parasiet. Ons data het egter aangetoon dat 'digtheidonderkompensasie' effektief was op die populasievlak wat 'n groter kiemkragtige saadproduksie per hektaar en gevolglik potensieel hoër 'nabrand'-saailinggetalle in digte stande as in yl stande tot gevolg het. Dit is teenstrydig met onlangse navorsing op protea-gemeenskappe wat in herfs gebrand is en laer saailinggetalle in digte stande as yl stande aantoon. Daar is afgelei dat die seisoen waarin gebrand is, die bepalende faktor was in 'nabrand'-aanwins van saailinge in stande van *P. lepidocarpodendron* wat ons bestudeer het. Die aantal struikstratumspesies m^{-2} het aansienlik afgeneem met 'n toename in digtheid van die *Protea* kruinstratum. Hierdie interaksie kan lei tot plaaslike uitsterwing van struikstratumspesies as gevolg van brand wat 'n vermeerdering van plante en gevolglik boskasievorming van kruinstratum proteas tot gevolg het.

Keywords: Cone production, density effects, Proteaceae, seed production, species richness

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Introduction

Proteoid fynbos is one of the most extensive structural formations in the Cape fynbos shrublands of southern Africa (Campbell 1986). This formation is characterized by an overstorey of non-sprouting, serotinous (canopy-stored seed) shrubs (1–4 m), all belonging to the Proteaceae and hereafter referred to as proteoids. These shrublands burn at intervals of 5 to 40 years and fire is a major selective force determining life histories of the component species (Cowling 1987).

Fire is also a major cause of density-independent variation in population size of these species (Bond *et al.* 1984). Different fires may result in different levels of recruitment as determined by a range of interacting density-dependent and -independent factors operating on different demographic parameters. Sizes of pre-fire seed banks, and therefore potential recruitment, vary with plant age, pre-fire density and pre-dispersal seed predation (Bond 1980; Le Maitre 1988). Recruitment is

also affected by post-fire factors such as post-dispersal seed predation, seedling predation and climatic conditions inimical to germination and seedling survival (Bond 1984).

Adult densities of proteoid shrubs in 12- to 20-year-old (mature) proteoid fynbos may range from zero (local extinction) to dense thickets up to 84 000 plants ha^{-1} (Bond *et al.* 1984). Several studies have inferred that pre-fire parent density is a major determinant of post-fire population size in Proteaceae. Bond *et al.* (1984) noted a decline in post-fire seedling recruitment (seedling-to-parent ratios) in southern Cape fynbos for several proteoids at pre-fire densities between 1 500 and 3 000 stems ha^{-1}. Le Maitre (1988) observed a negative relationship between pre-fire density and post-fire seedling-to-parent ratios for *Leucadendron laureolum* in the south-western Cape: this effect was apparent at densities of between 2 000 and 4 000 plants ha^{-1}. Since these studies did not present data on density effects on seed production per plant or per unit area, these effects could only be inferred. It may be possible that the absolute numbers of seedlings which establish after fires in dense stands could be higher than in sparse stands, even though seedling-to-parent ratios are lower in the former. This could be the result of density under-compensation, where reproductive output per plant declines with increasing density but increases per unit area (since output per plant is under-compensated for the increases in density) (Begon & Mortimer 1986).

Pre-dispersal seed predation by insects is another factor which could limit the size of seed banks and hence the post-fire recruitment levels of proteoids (Le Maitre 1988). It is possible that the incidence of pre-dispersal seed predation would increase with plant density, associated with a reduction in predator search times (Root 1973; Forcella 1980; De Stephen 1983; Greenwood 1985). An ancillary hypothesis would be that, as a means of eluding predation, variation in annual cone (and seed) production would increase with increasing density.

We studied the effects of density on the fecundity of *Protea lepidocarpodendron* (L.) L., a serotinous, non-sprouting species endemic to a small region of the south-western Cape. Rourke (1980) describes this species as 'gregarious, almost invariably growing in dense stands'. In our study area on the Cape Peninsula, *P. lepidocarpodendron* populations range from sparse stands to dense impenetrable thickets. We asked the following questions: Does fecundity, as measured by cone and seed production per plant, decline with increasing density? What is the effect of density on cone and seed production per unit area? Does the incidence of pre-dispersal predation by insects increase with increasing density? If so, does the variation in annual cone production show a parallel increase (Forcella 1980)? We addressed these questions by quantifying seed bank characteristics in three similar-aged *P. lepidocarpodendron* stands of different densities. We also determined the effect of proteoid overstorey density and hence cover, on understorey species richness. The current fire management policy for proteoid fynbos is designed to maximize the recruitment of non-sprouting proteoids (van Wilgen 1984). We argued that the supression of understorey species by overstorey proteoids could significantly reduce within-community species richness (Specht & Morgan 1981).

Methods

Sixteen-year-old dense (22 480 ha^{-1}), moderately dense (2 080 ha^{-1}) and sparse (160 individuals ha^{-1}) *Protea lepidocarpodendron* stands were sampled on the Cape Peninsula, south-western Cape. All sites were at roughly the same altitude, receiving a predominantly winter rainfall of about 1 000 mm yr^{-1} and having deep, rocky, Hutton form soils. The sparse site was on granite-derived soils above Camps Bay, whereas the other two were in the Silvermine Nature Reserve on ferricrete-derived soils. *P. lepidocarpodendron* was the only overstorey shrub species at each site.

The number of *P. lepidocarpodendron* individuals was counted at each site in five randomly located 5 × 5 m quadrats. Ten shrubs per site were randomly chosen. We measured basal diameter (at ground level), height and canopy cover of each shrub. The number of current (0-year-old), 1-, 2- and older than 2-year infructescences or cones were counted for each individual. Cone age determinations, estimated from node counts (Bond 1985), were only reliable for cones less than 3 years old. Five cones of each age category (0, 1, 2, >2 yrs) were harvested from each individual and placed in an oven at 50°C for 5 days until all seeds had been released. Numbers of 'plump' (assumed viable), aborted and predated seeds per cone were counted. Aborted seeds were cut open to ensure that no endosperm was present. Germination trials (of combined seed age groups) detected no differences in viability of plump seeds between stands. In all cases, germination percentages were high (80–90%, n = 60 seeds), indicating that methods for sorting viable from non-viable seeds were effective.

In order to measure the effects of density on species richness, we counted all vascular plant species present in each of ten 1 × 1 m quadrats, randomly located at each site. In fynbos vegetation, plots of this size are unlikely to incorporate significant environmental variation, and therefore measure point diversity (Whittaker 1977) which reflects biological determinants (e.g. competition) of richness (Bond 1983).

Results

In *Protea lepidocarpodendron*, there was a significant relationship between plant size and fecundity, as measured by cone production (Figure 1). Individuals in the sparse stand had a canopy coverage approximately three times greater than those in the dense stand, but only marginally greater than individuals in the moderately dense stand (Table 1). Cone production per plant in the sparse stand was twice and four times the value for the moderately dense and dense stands respectively. Seed set in the sparse stand was higher than that in the other stands. Plump seed numbers per plant in the sparse stand were four times and 30 times higher than in the

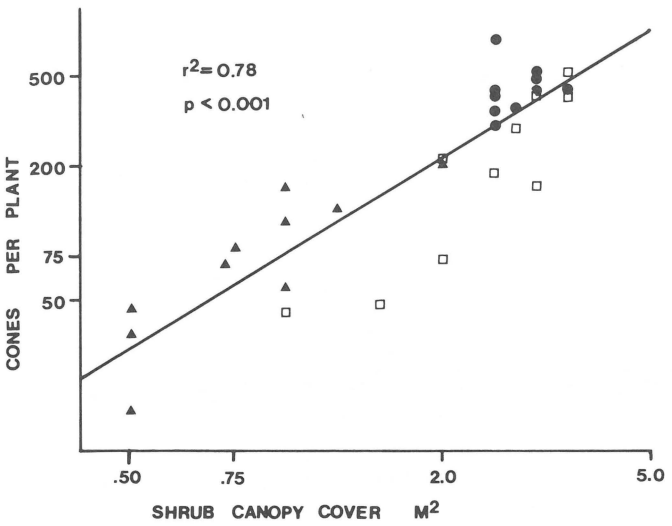

Figure 1 **Relationship between cone production and individual shrub canopy cover (m^2) for pooled individuals of** *Protea lepidocarpodendron* in sparse (●), moderately dense (□) and dense (▲) stands.

moderately dense and dense stands respectively. The numbers of plump seed per plant declined much more with density than did the number of cones per plant. Reproductive allocation in terms of fresh weight per plump seed was higher in the moderately dense stand.

In all stands, cone and plump seed production increased with plant age (Table 2) (i.e. plants were 14 years old when 2-year cones were formed). This was especially true of plants in the sparse stand. The coefficient of variation for both annual cone and plump seed production over 3 years was generally higher in the denser stands (Table 2).

The total number of seed produced per cone was lowest in the dense stand, but total seed production was the most variable as shown by the high coefficient of variation over 3 years (Table 3). The dense stand had the highest incidence of pre-dispersal seed predation per cone, and the highest coefficient of variation for this variable (Table 3). Similarly, there was an increase in numbers of predated seed per shrub with increasing density (Table 1). Incidence of pre-dispersal seed predation tended to increase with cone age for all stands (Table 3). All seed predators found were insects, mostly Lepidopteran borers (Myburgh *et al.* 1973), although these were not collected. Higher numbers of plump seeds per cone were recorded for the moderately dense and sparse stands. Coefficients of variation for percentage plump seed per cone over 3 years were high for all sites, although the most extreme values were recorded

Table 1 Physiognomic, reproductive and demographic traits of *Protea lepidocarpodendron* in three stands of differing densities on the Cape Peninsula. Data from ten individuals in each stand are expressed as means ± *S.D.*

Variable	Dense	Moderately dense	sparse
No. individuals ha^{-1}	22 480±5 473	2 080±657	160±89
Stand canopy cover (%)	88	15	1
Mean shrub canopy cover (m^2)	1.0±0.7	2.5±0.8	2.8±0.3
Mean shrub height (m)	2.7±0.7	1.9±0.4	2.1±0.4
Mean basal diameter (mm)	61.0±13.0	112.0±45.0	106.0±33.7
No. cones/plant	91.2±58.6	238.4±172.2	450.8±117.6
No. plump seed/plant	40.6±32.5	302.9±260.7	1 302.2±776.9
No. aborted seed/plant (%)	70.8±21.4	79.1±7.6	84.9±8.8
No. predated seed/plant (%)	28.9±21.6	19.9±7.3	13.2±8.7
No. plump seed/plant (%)	0.4±0.4	1.0±0.9	2.0±1.1
Plump seed weight (mg)	0.034±0.008	0.042±0.005	0.0384±0.007
Degree of serotiny*	38.9±18.5	34.4±25.3	58.8±28.0
Seed set (%)**	1.7±2.8	1.6±1.9	3.5±6.2
No. plump seed ha^{-1}	910 000	630 000	208 000

*Serotiny measured as contribution of current (year 0) plump seed bank to total plump seed bank (the greater the value, the lower the degree of serotiny)

**Seed set = 100 (no. seeds/no. ovules) in 17 non-predated year-0 inflorescences

Table 2 Variation in seed bank characteristics of *Protea lepidocarpodendron* in dense (22 480 plants ha^{-1}), moderately dense (2 080 plants ha^{-1}) and sparse (160 plants ha^{-1}) stands (n = 10 individuals). Data are means ± *S.D.*

Cone age (yr)	Cones per plant			Plump seed per plant		
	Dense	Moderately dense	Sparse	Dense	Moderately dense	Sparse
0	16.5±14.5	70.1±56.7	171.2±62.2	16.3±18.5	115.8±118.1	881.2±722.2
1	10.8±8.2	42.3±34.9	109.2±41.7	5.5±12.3	75.9±66.2	202.2±282.5
2	8.0±7.6	25.8±22.5	52.0±22.5	5.7±8.5	49.6±47.5	120.2±112.0
*C.V.**	94.1	91.9	59.5	155.2	105.2	139.0
>2**	55.9±34.5	100.2±69.6	118.4±38.7	13.1±18.3	61.5±83.8	98.7±119.4

*Coefficient of variation between plants for years 0–2

**Group comprising all cones older than 2 years

Table 3 Seed production in different-aged cones of *Protea lepidocarpodendron* in dense (22 480 plants ha^{-1}), moderately dense (2 080 plants ha^{-1}) and sparse (160 plants ha^{-1}) stands. Data are means ± *S.D.*, *n* = 50 cones per age class

	Seeds per cone								
	Total			Plump (%)			Predated (%)		
Cone age (yr)	Dense	Moderately dense	Sparse	Dense	Moderately dense	Sparse	Dense	Moderately dense	Sparse
0	128.9±48.1	158.2±20.4	166.7±19.1	0.8±0.8	1.3±1.5	3.0±2.0	35.0±25.1	16.5±9.6	8.4±11.7
1	159.7±17.3	163.7±20.6	138.2±15.5	0.2±0.4	1.9±2.3	1.5±1.7	40.6±27.8	24.5±22.5	16.4±13.0
2	116.2±67.0	168.2±29.8	152.2±20.3	0.6±1.2	2.0±2.8	1.4±1.0	20.6±12.8	29.1±11.7	27.4±28.5
*C.V**	37.4	14.4	14.0	160.4	127.9	88.2	95.2	75.2	116.4
>2**	88.2±43.5	137.7±49.4	137.1±32.3	0.2±0.2	0.8±0.8	0.7±0.9	36.3±22.8	21.3±12.6	26.0±26.7

*Coefficient of variation between plants for years 0–2

**Group comprising all cones older than 2 years

for the dense stand (Table 3).

Despite a density-dependent decline in reproductive output of individual *P. lepidocarpodendron* shrubs, seed production per hectare was 4.5 times higher in the dense, and more than 2 times higher in the moderately dense, than in the sparse stand (Table 1).

Point diversity declined with increasing density of *P. lepidocarpodendron* individuals. The number of species per m^{-2} (x ± *S.D.*) for the dense, moderately dense and sparse stands were 8.0 ± 3.2, 11.4 ± 2.4 and 20.2 ± 3.9 respectively.

Discussion

Our data provide evidence that for *Protea lepidocarpodendron,* reproductive output per plant declined with increasing density. This decline is probably a result of the smaller size of crowded individuals due to intraspecific competition for limited resources (Harper 1977; Antonovics & Levin 1980; Bond *et al.* 1984; Le Maitre 1988).

The incidence of pre-dispersal predation tended to increase with plant density. This is consistent with the resource concentration hypothesis (Root 1973) which predicts a negative relationship between predator search times and predation levels. This hypothesis predicts that in dense stands, search times are likely to be shorter and, therefore, predation levels are higher. Data were also consistent with the ancillary hypothesis which predicted that, as a means of eluding predation, variation in annual cone and seed production would increase with increasing density (Forcella 1980).

Two factors have been identified as the major determinants of post-fire population size in Proteaceae: pre-fire parent density and season of burn. Our data suggest that density under-compensation is effective at the population level, resulting in greater seed production per hectare in the dense than in the sparse sites. On the basis of viable seed availability, and assuming a favourable autumn burn, we would therefore expect highest post-fire seedling numbers in our densest stand, despite a much lower seedling-to-parent ratio. This contradicts the results of Le Maitre (1988) who found lower seedling numbers in dense (*ca.* 4 000 stems ha^{-1}) than sparse (*ca.* 300–600 stems ha^{-1}) stands of *Leucadendron laureolum* after summer and autumn burns. Is *P. lepidocarpodendron* peculiar in its ability to sustain high seed production per unit area in very dense stands? The species is confined to relatively heavy granite-, shale- and ferricrete-derived soils which are disjunct habitats of low coverage within its geographic range. In this species, the ability to sustain density-dependent reproductive output at such high densities may have evolved to prevent local extinction on these small and disjunct habitats. Neither Bond *et al.* (1984) nor Le Maitre (1988) provide comparable data on the effects of density on reproductive output for the proteoids they studied. Therefore, in their case, it is not possible to determine with certainty whether lower recruitment is the result of smaller pre-fire seed banks due to density-dependent intraspecific competition, or seed predation (see above), or to density-independent factors such as the dispersal of seeds out of the population.

The possibility remains, however, that for *P. lepidocarpodendron* density effects would be more important at higher population densities. Bond *et al.* (1984) have recorded *Protea* stand densities of up to 84 000 plants ha^{-1}. Age of stand may also be important since, with the onset of population senescence, the age-specific decline in reproductive output is generally faster in dense than sparse stands (Bond *et al.* 1984; Le Maitre 1988). Our data, however, indicated no age-specific decline in cone production, irrespective of stand density. We have to conclude, therefore, that season of burn rather than pre-fire parent density would be the most important determinant of post-fire population size for the three *P. lepidocarpodendron* stands we studied. It is of fundamental importance that these different scales of reference (individual vs. population, mature vs. senescent) should be defined when discussing the effects of density on population regulation.

The pattern of declining point diversity with increasing density (and hence cover) of overstorey species is well

documented for Australian heathlands, analogous to fynbos (Specht & Morgan 1981). Current management of proteoid fynbos is to prescribe autumn burns (van Wilgen 1984) which promote recruitment of the proteoid overstorey species (Bond *et al.* 1984; van Wilgen & Viviers 1985). By reducing overstorey species richness, a dense proteoid overstorey may eliminate locally rare understorey species. Differential post-fire recruitment of fynbos species probably plays an important role in the maintenance of diversity in these species-rich communities (Cowling 1987). If the aim of management is to maintain diversity, then prescribed fire regime should not favour the continued persistence of dense proteoid overstorey thickets.

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